Captive Propagation, Reproductive Biology, and Early Life History of *Etheostoma wapiti* (Boulder Darter), *E. vulneratum* (Wounded Darter), and *E. maculatum* (Spotted Darter)

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Abstract - Reproductive biology and early life-history data are important for understanding the ecology of fishes. In 2008, we conducted captive propagation studies on 3 species of darters of the subgenus *Nothonotus*: *Etheostoma wapiti* (Boulder Darter), *E. vulneratum* (Wounded Darter), and *E. maculatum* (Spotted Darter). The length of spawning period and associated range of water temperatures for the Wounded Darter exceeded that of the Spotted Darter and Boulder Darter. The mean number of eggs produced per female was lowest for Boulder Darter and highest in the Wounded Darter. The Boulder Darter had the highest percent of eggs hatched, the lowest percent larval to juvenile stage survivorship, and the lowest mean number of juveniles produced per female. Egg diameters at deposition and prior to hatch were smallest for the Spotted Darter. If reproductive biology and early life-history information from captive fishes represent that of wild populations, then the data obtained during this study are relevant to development and implementation of conservation and management plans for these closely related darter species.

Introduction

Etheostoma wapiti Etnier and Williams (Boulder Darter), *E. vulneratum* (Cope) (Wounded Darter), and *E. maculatum* Kirtland (Spotted Darter) are members of the *E. maculatum* species group of the darter subgenus *Nothonotus* (Etnier and Williams 1989, Near and Keck 2005). *Nothonotus* has been proposed as a genus-name elevation (Near and Keck 2005), but reason to retain *Etheostoma* was provided in Page et al. (2013). Species within this group are of conservation concern, in part, because of narrow or fragmented distributional ranges. All 3 species are allopatric across their ranges. Boulder Darters are found only within the Elk River drainage in Tennessee and Alabama (Etnier and Starnes 1993). Wounded Darters are found within the upper Tennessee River drainage in North Carolina, Tennessee, and Virginia. Spotted Darters are present in isolated populations within 6 states: Indiana, Kentucky, Ohio, New York, Pennsylvania, and West Virginia (Page and Burr 2011). The 3 species typically inhabit areas within or near riffles of medium-to-large rivers (Etnier and Starnes 1993, Osier and Welsh 2007). Conservation efforts for these species would be enhanced by studies on reproductive biology, such as captive-propagation studies that examine water temperature

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ranges of the spawning period, clutch sizes, and egg and larval survival and development (Rakes et al. 1999).

General reproductive strategies are known for the *E. maculatum* species group. Spawning females clump eggs in a male-guarded nest (Etnier and Williams 1989, Page 1983). Typically, the male-selected spawning site is within a riffle or near a riffle head and often includes 2 large rocks, 1 perched at an angle on top of another. These 2 stacked rocks provide a "V-shaped" space for egg deposition by females. The female clumps adhesive eggs on the ventral surface of the top rock and near the V-shaped junction of the 2 rocks. Like many other nest-guarding darter species, such as the *Catonotus* species group, there may be more than one female contributing eggs to a single nest (Etnier and Starnes 1993, Page et al. 1992). Although the general reproductive strategies are known, little information is available for many early life-history parameters associated with eggs and larvae.

The primary goal of this study was to document and qualitatively compare parameters associated with the reproductive ecology and early life history of the Boulder Darter, Wounded Darter, and Spotted Darter. Captive propagation of the species during the same year (2008) at the same facility allowed for among-species comparisons. Through captive propagation, it is possible to examine a suite of life-history parameters, such as clutch size, number of clutches, egg size, egg survival, hatch time, larval size, and larval survival. These life-history parameters are relevant to development and implementation of conservation and management plans (Rakes et al. 1999). However, we recognize that life-history parameters observed for captive fishes may differ from those of wild populations.

Methods

We conducted captive propagation of Boulder Darters, Wounded Darters, and Spotted Darters in 2008 at Conservation Fisheries, Inc. (CFI), Knoxville, TN. Breeding individuals of Boulder Darters (n = 27) included 20 individuals collected from the Elk River drainage in south-central Tennessee: 8 individuals in summer 2003 from Elk River, 8 individuals in spring 2007 from Elk River, 1 individual in fall 2006 from Richland Creek, and 3 individuals in spring 2008 from Richland Creek. Additionally, 7 captive-bred adults were included from previous years of production. Wounded Darters were represented by 16 adults collected from Little Tennessee River in North Carolina, downstream of Franklin during spring and summer 2007. Spotted Darters were represented by 18 adults collected from Elk River, WV, during February 2008. We housed each species in a separate recirculating system. Boulder Darters and Wounded Darters were in 1500-L systems consisting of twenty-seven 76-L (75 × 32 × 30 cm) aquaria with a 190-L sump (oval 130 × 90 × 50 cm). We housed Spotted Darters in an 850-L system of fourteen 76-L glass aquaria with a 190-L sump.

Photoperiod and water temperature during captive propagation mimicked seasonal changes. Photoperiod was controlled by an astronomic timer (Intermatic Next Generation Year Long Double Circuit Electronic Timer) operating 1.22-m fluorescent shop lights (with Daylight Deluxe and Cool White bulbs). We reduced water temperatures to a low of 2 °C during winter using fans to draw in outside air. During summer, we manipulated water temperatures with either outside air circulation or air conditioning to maintain levels below 25 °C using a programmable thermostat.

For all species, tanks were set up with a gravel–sand substrate and cover items consisting of ceramic slates, PVC pipes, and natural stone slabs. We created spawning sites with tiles or terra cotta slates (28.0–30.5-cm long and 15.3-cm wide) stacked together to form a horizontal "V" and spaced apart on the open end with 1.9-cm or 2.5-cm diameter PVC tubes. Filtration included individual tank sponge filters, airstones, and a biological filter (i.e., biotower) in each sump. We treated systems with salt (maintained at 1.5–2.5 ppt) to reduce fish stress and prevent parasitic infections.

We arranged breeding groups for each species with different male:female sex ratios depending on prior observed interactions when known. Boulder Darters were arranged in 11 breeding groups: 5 with 1:2 and 6 with 1:1. Multiple males per tank were not used for this species due to territorial aggression we witnessed in the past. We arranged Wounded Darters in 3 breeding groups each containing 2:2 because we have not witnessed excessive male aggression with this species. We arranged Spotted Darters in 3 breeding groups with ratios of 2:3, 1:2, and 1:1.

We set up incubation tanks (76-L aquaria), oval catch tubs (63.5 × 53.3 × 17.8 cm), and circular rearing tubs (70-cm diameter, 30-cm depth, and approximately 100-L capacity) in each species' recirculating system. Each rearing and capture tub was drained by a center vertical standpipe with a diameter of 2.7–3.5 cm and length of 10–15 cm. The standpipe was topped with a 7.5–10-cm widened PVC fitting encircled with a 250–500-μm screen. Water from incubation tanks flowed into catch tubs allowing for passive collection of emerging larvae. We transferred the captured larvae with a baster or pipette to a rearing tub. Water flowed into the rearing tub through a 1.9-cm PVC pipe fitted with a drilled end cap. Specifically, the drilled end cap (4-mm hole) generated a swift, fine surface stream that created circular flow, but with reduced overall water turnover within the tub. Reduced water turnover allowed for increased food retention within the tub. Flexible airstones encircled the base of each standpipe. These airstones created water flow away from the standpipe, thereby preventing larval impingement on the standpipe screens.

Adult breeders, larvae, and juveniles required different feeding regimes. Adult darters were fed live *Lumbriculus variegatus* (Blackworm), live *Daphnia pulex* Leydig (Common Water Flea), frozen bloodworms (chironomids), and frozen adult brine shrimp (*Artemia*). Food quantities were determined by water temperature, fish activity levels, and the willingness of fish to feed. An automatic feeder with a reservoir, timer, and solenoid dispensed food into the rearing tub during the day. The feeding reservoir was an 11.4-L opaque plastic tub (30 × 20 × 28 cm) with a solenoid-controlled bottom spout. The feeding reservoir was filled with water from the system, then with 15-mL concentrated *Brachionus* rotifers, 15-mL diluted (1 part algae to 20 parts water) Nanno 3600 ™ *Nannochloropsis* sp. (Instant Algae® produced by ReedMarineculture Inc.), 15-mL newly hatched brine shrimp nauplii, and 15-mL concentrated *Ceriodaphnia dubia* Richard (a water flea) neonates. The timer-controlled solenoid dispensed food for 8–10 seconds every 2 minutes during daylight hours. To supplement the reservoir feeding, we lightly dusted several food powders on top of the rearing tub 2–4 times daily. The powders consisted of equal parts from a premixed batch: A.P.R., Artificial Plankton–Rotifer (Ocean Star International, Inc.); Larval AP100, <100 µm and 100–150 µm (Zeigler Bros., Inc.); and Spirulina (Salt Creek, Inc.). As larvae grew and transformed into benthic juveniles, they were subsequently separated from younger larvae and transferred to 76-L tanks. We supplemented juveniles with larger food items such as chopped Blackworms and frozen chopped bloodworms.

We recorded the duration and water temperatures of spawning periods as well as the egg and larval characteristics for each species, including data on egg production, clutch size, mean number of eggs per female, number of eggs per breeding group, egg size at deposition, egg size prior to hatch, and percent of eggs hatched. We determined the duration of the spawning period by the first and last day of egg production for each species. We photographed subsamples of eggs, yolk-sac larvae, developing larvae, and transformed juveniles with a Canon Rebel® DSLR camera with Canon microscope lens mount fitted on a Nikon dissecting scope, and recorded photogrammetric measurements for eggs, yolk-sac larvae, developing larvae, and juveniles. We also used the photographs for myomere counts of 12–18-day-old larvae and for determining fin development stage of larvae. Eggs were measured (nearest 0.1 mm) across the minor and major axis at hatch and just prior to hatch. Total lengths (TL) of larvae at hatch and at yolk sac absorption were measured to the nearest 0.1 mm, and those of larvae at start of fin development were measured to the nearest 0.5 mm. We documented age (days) at the start of first fin development and calculated the percent survivorship of pelagic larvae to benthic juveniles, as well as the length (TL, nearest 0.5 mm) and age (days) of fully transformed juveniles (Simon and Wallus 2006).

Our analytical approach was not based on hypothesis testing, but rather focused on parameter estimates and descriptive statistics including means, percentages, and ranges. Variance estimates could not be calculated for mean eggs per female and mean juveniles per female because we were not able to separate individual-female contributions to the number of eggs in a nest. We reported ranges (minimum and maximum values) and among-species differences for data on egg sizes, larval lengths, myomere counts, and ages.

Results

Boulder Darter

Boulder Darters spawned during a 48-day period (25 April–11 June 2008) within a water temperature range of 17–22.5 °C (Table 1, Fig.1). From the 11 breeding groups, 2614 eggs were collected. The mean number of eggs produced per female was 163. Breeding groups with 1 male and 2 females produced a total of 1317 eggs (mean = 132 eggs per female), and those with a single male and single female produced a total of 1297 eggs (mean = 216 eggs per female). Ages of most breeding individuals were unknown, but some individuals had been retained for breeding for

Table 1. Reproductive biology and early life-history parameters of *Etheostoma wapiti* (Boulder Darter), *E. vulneratum* (Wounded Darter), and *E. maculatum* (Spotted Darter) from a captive-propagation study during 2008 (*n* = sample size).

	E. wapiti		*E. vulneratum*		*E. maculatum*	
Parameter	*n*	Value	*n*	Value	*n*	Value
Spawning period (days)		48		89		46
Spawning water temperatures (°C)		17.0–22.5		16.0–24.0		17.0–22.5
Mean number of eggs/female	16	163	6	345	6	207
Percent egg hatch		68.1%		34.3%		57.3%
Percent larval to juvenile stage survivorship		54.4%		76.0%		72.4%
Percent total survivorship		37.0%		26.0%		41.4%
Mean number of juveniles produced per female	16	61	6	90	6	86
Egg diameter at deposition (mm)	4	2.2–2.4	3	2.1–2.3	2	1.9–2.0
Egg diameter prior to hatch (mm)	7	2.4–2.6	8	2.2–2.5	10	1.9–2.1
Larvae length at hatch (mm)	3	8.5–9.1	2	7.8–8.0	4	6.7–7.0
Larvae length at yolk sac absorption (mm)	4	9.5–9.6	3	9.7–9.8	6	8.0–8.4
Myomere count of larvae	17	37–39	19	35–39	17	33–35
Larvae length at start of fin development (mm)	5	14.0–15.0	5	13.5–14.0	5	12.0–13.0
Age at first fin development (days)	5	14–16	5	12–14	5	14–16
Length of juvenile (mm)	5	16.0–17.0	5	16.5–17.5	5	16.0–17.0
Age of full transformation (days)	5	19–21	5	18–22	5	19–21

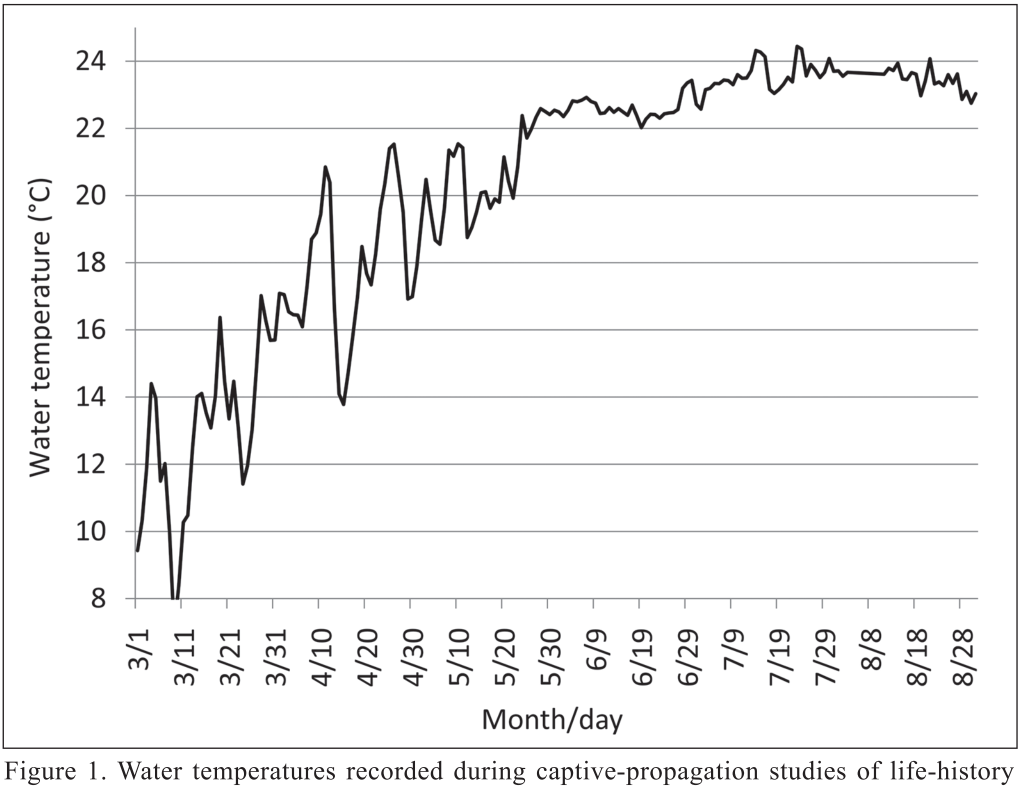

Figure 1. Water temperatures recorded during captive-propagation studies of life-history parameters of Boulder Darters, Wounded Darters, and Spotted Darters during March–August 2008.

several years at CFI and could have been as old as 6 years. A total of 1779 eggs hatched (68.1%), and 968 juveniles were produced. Survivorship of pelagic larvae transformed to benthic juveniles was 54.4%, and the total survival rate from eggs to juveniles was 37.0%. The mean number of juveniles survived per female was 61.

Egg size was 2.2–2.4 mm at spawn and 2.4–2.6 mm prior to hatch (Figs. 2A–B). Larvae at hatch ranged 8.5–9.1 mm TL with a yolk sac (Fig. 2C). Larval size at yolk-sac absorption was 9.5–9.6 mm TL. Transformation of fins on larvae started 14–16 days post hatch. Larval size ranged 14.0–15.0 mm TL at the time of initial development of first dorsal fin (Fig. 2D). Full transformation of larvae to juveniles, including a fully developed first dorsal fin, was completed by 19–21 days post hatch, at which time they ranged 16.0–17.0 mm TL and were fully benthic (Fig. 2E). The dorsal myomere count for larvae ranged 37–39 ($n = 17$) with a mode of 38.

Wounded Darter

Wounded Darters spawned during an 89-day period (21 April–18 July 2008) within a water temperature range of 16.0–24.0 °C (Table 1, Fig.1). The 3 breeding groups varied in production from 187 to 448 eggs per female (mean = 345). Female ages were unknown, but were estimated at 2–3 years. Out of 2070 eggs produced, 709 larvae were transferred from the catch tub to the rearing tub, representing a hatch rate of 34.3%. Of these 709 larvae, 539 transformed into juveniles and were transferred to tanks for grow out, representing a survival rate of 76.0% from pelagic larvae to benthic juveniles. Survivorship from egg to juvenile was 26.0%. The mean number of juveniles survived per female was 90.

Egg size was 2.1–2.3 mm at spawn and 2.2–2.5 mm just prior to hatch (Fig. 2F, G). Hatch times for eggs laid in late April were 7–9 days; however, hatch times generally decreased as temperatures increased during the spawning season. Larval size at hatch was 7.8–8.0 mm TL (Fig. 2H). Larval size at yolk-sac absorption was 9.7–9.8 mm TL. Transformation of fins on larvae started 12–14 days post hatch. Larval size ranged from 13.5–14.0 mm TL at the time of initial development of first dorsal fin (Fig. 2I). Full transformation of larvae to juveniles was completed by 18–22 days post hatch, at which time they ranged 16.5–17.5 mm TL and were fully benthic (Fig. 2J). Dorsal myomere counts on larvae ranged 35–39 ($n = 19$) with a mode of 37.

Spotted Darter

Spotted Darters spawned during a 46-day period (29 April–13 June 2008) within a range of water temperatures of 17.0–22.5 °C, with spawning initiated at 17.0 °C (Table 1, Fig.1). Spotted Darter females produced 1247 eggs, ~207 per female. The mean number of eggs per female in the different male:female sex-ratio groups were: 251 for the 2:3 group, 114 for the 1:2 group, and 265 for the 1:1 group. A total of 714 larvae were transferred from the catch tub to the rearing tub, representing a hatch rate of 57.3%. Of these 714 larvae, 517 transformed into juveniles, resulting in a survivorship of 72.4%. The total survivorship of Spotted Darters from egg to juvenile was 41.4%. The mean number of juveniles that survived per female was 86.

Egg size was 1.9–2.0 mm at spawn and 1.9–2.1 mm just prior to hatch (Fig. 2K–L). Larval Spotted Darters at hatch were approximately 6.7–7.0 mm TL and had

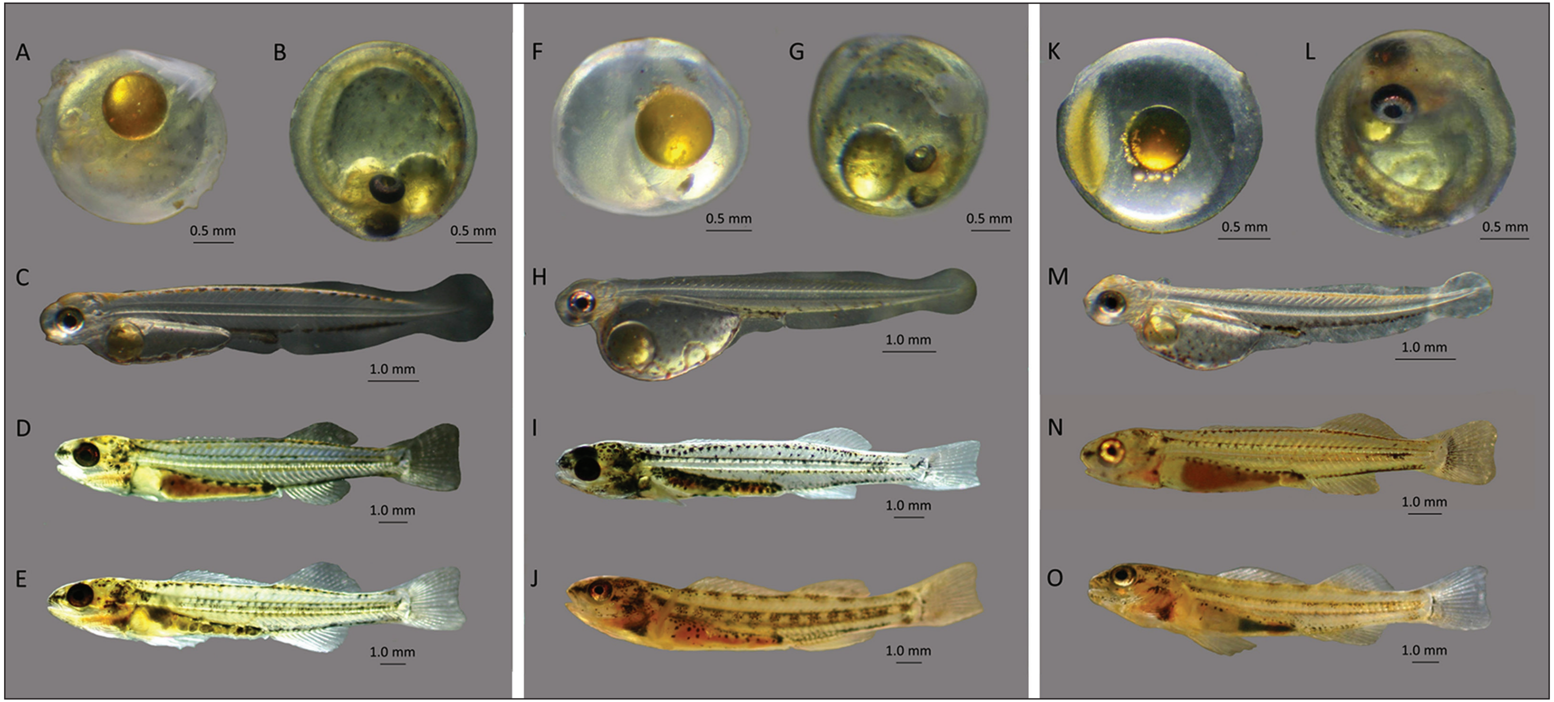

Figure 2. Photographs of early eggs, eggs close to hatch, yolk-sac larvae, larvae during fin development, and fully transformed juveniles for *Etheostoma wapiti* (Boulder Darter; A–E), *E. vulneratum* (Wounded Darter; F–J), and *E. maculatum* (Spotted Darter; K–O).

heavy yolk sacs (Fig. 2M). Size at yolk-sac absorption was 8.0–8.4 mm TL. Transformation of fins on larvae started 14–16 days post hatch. Larval size ranged 12–13 mm TL at the time of initial development of first dorsal fin, and dorsal myomere count was 33–35 (n = 17) with a mode of 35 (Fig. 2N). Full juvenile transformation of larvae was completed by 19–21 days post hatch, at which time they ranged 16–17 mm TL and were fully benthic (Fig. 2O).

Discussion

Boulder Darter

For the Boulder Darter, the relatively large egg diameter prior to hatch may partly explain the higher egg hatch rate and larger larval length at hatch. Although larger, more robust larvae may have an advantage over smaller larvae for survivorship (Kamler 2005), the Boulder Darter had the lowest percent larval-to-juvenile stage survivorship. Boulder Darter egg production per female was lower than that observed for the other 2 species. If this pattern of low egg production also occurs in a wild setting, then the Boulder Darter reproductive strategy may involve an increased female investment in each egg, thus producing fewer, but larger eggs and larvae. Boulder Darter larvae emerged with a much-reduced yolk sac as compared to the Wounded and Spotted Darter larvae. This finding may suggest that the Boulder Darter larvae are more developed than the other 2 species at the critical stage of emergence and first feeding. This increased larval size may also account for the Boulder Darter larvae spending less time in the water column relative to that of Wounded and Spotted Darters; Douglas et al. (2013) reported a mean pelagic larval duration of 14 days for Boulder Darter, relative to 17.5 days for Wounded and Spotted Darters. The use of benthic habitat before full juvenile transformation may be related to the larger larval size of the Boulder Darter. The energetic cost of constantly swimming at that size may not be an effective foraging method. Larvae may forage benthically with small swimming bursts rather than staying pelagic all the time, thereby conserving energy.

Wounded Darter

Captive propagation results were similar to field observations of Stiles (1972). Stiles (1972) reported spawning of Wounded Darters in the Little River, TN, from the last 2 weeks of May to the last week of July with water temperatures ranging 16.0–20.0 °C. In the current study, Wounded Darters had a relatively low hatch rate as well as a low survival rate from egg to juvenile, whereas the percent larval to juvenile stage survivorship of the Wounded Darter was highest among the 3 species. The low hatch rate of Wounded Darter eggs was influenced by egg infertility as well as failure of heavy yolk-sac larvae to thrive. Poor water quality may have been an issue due to heavy organic build-up in the system from the automatic larval feeder. The egg-to-juvenile survival rate of 26% seems unusually low for this species, but we do not have a comparative estimate for this rate for wild populations. The larval survival rate (76.0%) of this species, however, was substantially higher than that of egg survivorship. Increasing temperatures may have had a negative effect on egg and larval survivorship (Brooks et al. 1997). Temperature rises were associated with decreased incubation time. This decreased incubation time possibly caused premature hatching.

Our data suggest that the Wounded Darter reproductive strategy relies on producing a large number of eggs that result in less-developed larvae and an early emergence. Wounded Darter larvae emerged with the largest (least-absorbed) yolk sac compared to the other study species, suggesting that the larvae are the least developed at hatching and first emergence, possibly making them susceptible to relatively greater mortality during this stage (Fig. 2C, H, M). The heavy yolk sac at hatch was observed to hamper swimming ability, as larvae were seen lying on the bottom for at least a day after initial emergence. Lack of consistent mobility just after emergence could leave the yolk-sac larvae susceptible to infection or predation. Further, the decreased swimming ability of the heavy yolk-sac larvae may increase dispersal rates because larvae may drift much greater distances before holding position in current. Consequently, there may be population-level advantages to underdeveloped larvae at hatch (Miller et al. 1988) because increased larval dispersal abilities, associated with less-developed larvae at hatch, may result in higher gene flow (Turner 2001, Turner and Trexler 1998).

Spotted Darter

Our observations on Spotted Darters were generally consistent with those of Raney and Lachner (1939), who reported that the breeding season in the upper Allegheny River drainage extended from the last week in May to the end of June. Further, Raney and Lachner (1939) noted a water temperature of 17.8 °C during the spawning period. In the current study, the Spotted Darter spawned during a 6-week period (29 April–13 June) with water temperatures ranging 17–22.5 °C. Egg size (2 mm) and clutch size (140–352 eggs) reported by Raney and Lachner (1939) were also consistent with our results. Filial cannibalism, which was reported by Raney and Lachner (1939), may have been present during our study resulting in biased egg counts. The length range (5.0–6.0 mm TL) of newly hatched larvae reported by Raney and Lachner (1939) was slightly less than that of our study (6.7–7.0 mm TL); however, general descriptions of larvae, including a heavy yolk sac, were consistent for both studies.

Survival rates of eggs and larvae of the Spotted Darter were intermediate to those of Boulder and Wounded Darters. Egg to juvenile survival rate (41.4%) of the Spotted Darter was very similar to that of the Boulder Darter. Most of the losses of larvae happened in the last month when temperatures were higher, similar to the Wounded Darter losses. There were many possible explanations for these losses. Excessive feeding and water quality issues may have played a part in poor larval survivorship in late May through early June. Temperature rises were associated with decreased incubation time. This decrease in egg-incubation time may have contributed to premature hatching of eggs resulting in underdeveloped larvae. It is also possible that there could have been predation of the youngest larvae by the oldest within the rearing tubs (Ruble et al. 2014).

Of the 3 species, the Spotted Darter had the smallest eggs just prior to hatch, a finding consistent with that of Simon and Wallus' (2006) report that Spotted Darter larvae at hatch were smaller than those of the Wounded Darter. Further, Simon et al. (1987) depicted a single larva at hatch of 5.3 mm from the Tippecanoe River, IN, which was smaller than our captively propagated larvae. Given that the Spotted Darter has a relatively wide geographic range, it is likely that latitudinal effects may influence spawning time as well as egg and larva size (Hubbs 1985, Johnston and Leggett 2002). Although Spotted Darter eggs were smaller than both other species, newly hatched larvae were well developed with a moderate-sized yolk sac.

Differences in production across all species related to breeding group size and sex ratios were interesting but difficult to interpret. For Boulder Darters, the 1:1 pairings produced more eggs than that of the 1:2 groups. The Wounded Darter only had 3 breeding groups, set up in identical sex ratios (2:2). Two of the breeding groups had very similar production, but the third produced fewer eggs per female. There were 3 different sex-ratio groups used with the Spotted Darters. Two of these groups produced similar numbers per female (2:3 group produced 251, and 1:1 produced 265). The 1:2 breeding group produced less (114 per female). It is unclear if individual females' age/condition, size, or breeding-group dynamics more heavily influenced egg production. Females are expected to have individual variability in egg production (Morrongiello et al. 2012), but our study design was focused on breeding groups with multiple females, thus individual variability was not assessed. Also, it is possible that not all females spawned in lower-producing groups in the Wounded and Spotted darters. There may be negative interactions among females that prevent full productivity. In the future, it would be desirable to work with more replicates and better control of variables such as breeding-group dynamics, age of breeders, and size of breeders to determine true production potential of each species. Specifically, differences among breeding groups, as well as the use of different spawning substrates, inserted variation that was not accounted for in our current study design. Future studies that follow a controlled experimental approach are warranted to address these concerns.

Conclusions

From a biogeographic perspective, this research compared life-history parameters among 3 closely related species that are all allopatric, but differ in having northern and southern distribution ranges, narrow to relatively wide distribution ranges, and upland versus midland elevations. Although all 3 species employed the same K-selected reproductive strategy of male-guarded nests, differences were noted in the mean number of eggs produced per female, hatch rate, and survivorship of various early life stages when compared via captive propagation. These among- or between-species differences suggest slightly varying degrees of parental investment and variation in ontogenetic development.

The Boulder Darter and Spotted Darter produced fewer eggs per female and well-developed larvae relative to that of the Wounded Darter, but the survival rate to juvenile stage was lower in the Boulder Darter and Spotted Darter. Although the observed variations may, in part, be an artifact of captive-propagation conditions, they likely reflect subtle ontogenetic differences of each species that may help each survive in their different specific macro- and microhabitats. For example, darters that inhabit larger rivers with multiple habitat patches throughout the river might invest in a strategy that promotes increased dispersal ability. In contrast, darters that inhabit smaller rivers with fewer habitat patches might invest more in individual larval survivorship with reduced larval dispersal in order to stay in prime habitat.

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